

MY HOME IS YOUR CASTLE: ROOST MAKING IS SEXUALLY SELECTED IN THE BAT *LOPHOSTOMA SILVICOLUM*

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Shelters are important for the survival and reproduction of many animals and this is particularly true for bats. Depending on the future use and effect of shelters on the fitness of individuals, not all members of a group of animals may contribute equally to shelter making. Thus, knowledge about the identity of shelter-making individuals may teach us much about the social system and mating strategy of species. To exemplify this, we review what is known about the roost-making behavior and the social system of *Lophostoma silvicolum*, a neotropical bat that excavates roost cavities in active arboreal termite nests. Roosts in termite nests are highly beneficial for the bats because they offer improved microclimate and possibly are responsible for the lower parasite loads of *L. silvicolum* in comparison to bat species using other, more common, roost types. Examination of observational field data in combination with genetic analyses shows that roost cavities excavated by single males subsequently serve as maternity roosts for females and that this improves reproductive success of the male who excavated the roost. This suggests that roosts in termite nests serve as an extended male phenotype and roost making is a sexually selected behavior. Roost-making behavior is tightly linked to the species' social organization (single-male–multifemale associations that stay together year-round) and mating system (resource-defense polygyny). The case study of *L. silvicolum* shows that it is important to learn more about the implications of shelter making in bats and other animals from ongoing and future studies. However, differences in costs and benefits for each group member must be carefully evaluated before drawing conclusions about social systems and mating strategies in order to contribute to our current knowledge about the evolution of sociality in mammals.

Key words: extended phenotype, mating system, offspring dispersal, philopatry, reproductive success, resource-defense polygyny, sexual dimorphism, social system

Shelter making is comparatively rare in mammals and the resulting structures are often temporary and relatively simple (Hansell 1984). This is in contrast to other groups of animals such as birds or insects, which frequently engage in the making of elaborate refuges. Nonetheless, quality, availability, and distribution of roosts or nesting sites may limit the geographic range of mammals including many bat populations (Kunz and Lumsden 2003) and may influence their reproductive success (Racey 1973) as well as their population structure and social behavior (Kerth and König 1999; Kerth et al. 2000, 2001). Only a few studies on animals (Collias and Collias 1976; Forsythe 1989; Hansell 1984; von Frisch 1974), and especially

on bats (e.g., Chaverri et al. 2007; Kerth et al. 2001; Reckardt and Kerth 2007; Willis and Brigham 2007), have listed the advantages and disadvantages of refuges and linked them to the social systems of the species in question.

Building or modifying a refuge requires time and energy, costs that must be compensated by later benefits. In social animals, not all group members are expected to invest equally in the cost associated with shelter construction, maintenance, and defense (Collias 1964; Morrison 1979; Morrison and Morrison 1981). Individual investment should depend on the future use and indirect fitness benefits of a shelter by each group member. Consequently, we should often see sex differences in roost-making behavior. For example, females have to make shelters alone if males are living elsewhere or do not contribute because paternal care is not required for the successful rearing of offspring (Dawkins 1976; Hansell 1984). A male may share parental care or provide other services such as shelter construction if he thus gains biased access to mating

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(e.g., in case of postpartum estrus). In most terrestrial vertebrates, including mammals, males compete for females, whereas the latter choose their partners. Shelter making could serve as a form of extended male phenotype, enabling females to judge the quality of potential mates (Andersson 1994; Dawkins 1999). Extended phenotype is the effect genes may have on the environment through an animal's behavior, a famous example being beaver dams (Dawkins 1999).

Bats form the 2nd largest mammalian order, with most species living in the tropics. The more than 1,200 currently recognized species display a tremendous diversity in ecology, body size, diet, and social system (Kunz and Fenton 2003; McCracken and Wilkinson 2000; Nowak 1994). Despite pronounced ecological differences, most bats live in groups for at least some part of their annual life cycle. Size and composition of groups differ between species (Bradbury and Vehrencamp 1977; McCracken and Wilkinson 2000), but generally it is the females that are social and rear their young communally. Male bats are often solitary, they may join female maternity colonies, or, more rarely, form groups or colonies of their own (Encarnação et al. 2005; Safi 2008; Safi and Kerth 2007). Limited roost availability could generate pressure on bats to aggregate. However, bats living in groups might also gain individual benefits such as thermoregulatory advantages (e.g., Willis and Brigham 2007), decreased predation (e.g., Fenton et al. 1994), or cooperation among group members (e.g., Wilkinson 1984). Given the clear importance of day roosts in the lives of bats, it is surprising that relatively few bat species modify structures and construct their own roosts. Instead, most bats rely on naturally occurring cavities or shelters built by other animals (Kunz 1982; Kunz and Lumsden 2003). This is surprising because in primates nest making is associated with nocturnality and offspring that are left behind by the parents during foraging (Kappeler 1999), both of which behaviors are typical for most bats. In this paper, we review what is known about the roost-making behavior and the social system of *Lophostoma silvicolum*, a neotropical bat that excavates active arboreal termite nests to roost in them.

One strategy to improve roost availability and reduce competition for limited shelters is to use one built by another species. The phenomenon of living together with species that provide a refuge has been studied particularly well in arthropods. Examples range from ants inhabiting the oothecas of spiders (Dejean et al. 1999) to various arthropods inhabiting ant nests (Wilson 1971). The latter are particularly interesting because they are examples of species capable of inhabiting active ant colonies, which normally defend themselves aggressively against intruders. However, not only arthropods live in the nests of social insects. For example, the use of termite nests as shelters occurs in a large variety of birds (reviewed in Brightsmith 2000), some reptiles (e.g., *Varanus niloticus*—Cowles 1928), and mammals (e.g., *Herpestes*—Rasa 1985). Termites occur nearly worldwide and many species build elaborate nests or mounds, but secondary users of termite nests can only occur wherever the required termite host species is distributed.

Most mammals, such as mongooses that use termite nests, usually live in the ventilating channels of mounds and do not

modify the nest itself (e.g., Rasa 1985). Some bats species violate this general rule, including 1 vespertilionid (*Murina florium*—Clague et al. 1999), 1 flying fox (*Balionycteris maculata*—Hodgkison et al. 2003), and the entire neotropical genus *Lophostoma* (formerly *Tonatia*—Lee et al. 2002) as far as the roost choice is known (Goodwin and Greenhall 1961; Handley 1976; Kalko et al. 2006; McCarthy et al. 1992). The most common and well-known species of the genus *Lophostoma*, *L. silvicolum*, excavates active, arboreal nests of the termite *Nasutitermes corniger* (Kalko et al. 2006). The termite nests, which are made from predigested wood, cemented together with the termites' saliva, are very hard. Thus, the excavation of roosts is probably costly in terms of time and energy. To offset these costs it seems likely that termite mounds provide significant fitness benefits for the excavator.

There were several possible, potentially nonexclusive hypotheses to explain roost-excavation behavior in *L. silvicolum*. First, we expected that roosts in termite nests would be beneficial for the bats. One disadvantage of group living in bats is thought to be a higher transmission rate of ectoparasites. However, termites are known for their chemical defenses against other insects (Prestwich 1988) and we compared ectoparasite loads of *L. silvicolum* to those of a closely related species, *Tonatia saurophila*, which occupies a similar ecological niche, has similar group sizes, but lives in tree cavities. Finally, based on what is known about Old World termites, whose mound temperatures are warm and stable (Korb and Linsenmair 2000), we expected that the consistently round-shaped tree nests of *N. corniger* might also be advantageous concerning their microclimate.

Regarding the roost-making individuals, participation of both sexes in roost construction was only expected if males and females both provide parental care, which is extremely rare in bats. Therefore, 2 modes of selection during the evolution of roost making in *L. silvicolum* seemed possible: natural selection or sexual selection. In the case of roost making by females, natural selection could have promoted the evolution of this behavior if females cooperate in the excavation of roosts in termite nests. In contrast, sexual selection could have been the main driving force for roost making if excavated termite nests are a resource provided by males to attract females. Of course, in the latter scenario the male himself also might profit directly from the advantages a termite nest roost offers and natural selection might be an additional force promoting the evolution of this behavior. In both scenarios, we would expect that roosts in termite nests are beneficial for females for rearing their young. These 2 main different modes of selection on roost-making behavior result in different and testable sex-specific predictions, concerning group composition, behavior, morphology, reproductive success, and dispersal (Table 1).

If males were solely responsible for excavating termite nests, this would suggest that they benefit by attracting females to the resource they are providing. In this type of mating system, a resource-defense polygyny, females choose breeding roosts provided and defended by males and aggregate there. Possession of such roosts would improve male reproductive success, thereby balancing the costs of roost making.

TABLE 1.—Predictions concerning male and female behavior, genetic relatedness, and morphology depending on whether roost making is under sexual or natural selection.

	Sexual selection for access to mating partners	Natural selection for communal breeding
Both sexes		
Group composition	Single-male—multifemale	Only females, or brief male tenure
Excavation of roosts in termite nests	Males	Females
Males		
Sexual dimorphism	Males larger	No prediction
Condition of males	Successful males in better condition	No prediction
Reproductive success of nest-owning males	High; mating takes place in the roost	No prediction; mating may or may not take place in the roost
Reproductive skew among males	High	Low
Females		
Social interactions among females	No prediction; female groups may be anonymous aggregations with no or few social interactions	Social interactions; cooperation during roost making; individual or group recognition among females
Female philopatry	Low; female offspring leave the group and avoid mating with the father if male tenure is long	High; female philopatry stabilizes cooperation during roost making via kin selection or familiarity. If low, at least very stable groups are expected and cooperation during roost making should be stabilized via familiarity
Genetic diversity within female groups	No prediction	Low
Genetic structuring among female groups	Absent or low	High

According to Clutton-Brock (1989b) variance in male mating success is predominantly influenced by 3 variables: the effect of the male's contribution to parental care and thus the survival of his offspring; the defensibility of groups of females and degree to which a male is able to monopolize copulations; and the size, stability, and defensibility of female groups. Theoretically, the conditions favoring a polygynous mating system would be the following: little or no effect of paternal care, high defensibility of females, and high stability of female groups. However, many species do not fulfill this pattern so clearly and, depending on the availability of mating partners or resources such as food, roosts, or territories, there also may be variation within species (Schaal and Bradbury 1987).

Alternatively, females might cooperatively excavate termite nests to create roosts as suitable shelters to rear their offspring. In this case, sociality would be the result of females sharing a roost they made together, facilitating female philopatry and maternal structuring of groups (Kerth et al. 2000; König 1997).

In this paper, we review recent research on *L. silvicolium*, which made it possible to test the relevant parameters (Table 1) against each other and to put our conclusions in the context of mammalian mating systems in general.

BIOLOGY OF *LOPHOSTOMA SILVICOLIUM* AND STUDY SITES

The white-throated round-eared bat, *L. silvicolium* (Phyllostomidae), is medium sized (about 30 g at our study site in Panama—Dechmann et al. 2005), and characterized by extremely round-tipped, broad wings and large ears. This morphology is ideally suited for their gleaning foraging mode (Norberg and Rayner 1987). *L. silvicolium* feeds on large arthropods, particularly katydids (Tettigoniidae), which are

picked up from the vegetation and the ground. The bats hunt in small individual foraging areas in the proximity of their roosts (Bockholdt 1998; Kalko et al. 1999; Servatius 1997), are strictly forest dwelling, and are distributed throughout tropical Central America and part of South America (Reid 1997). Exclusive day roosts are arboreal, active termite nests of the species *N. corniger*, which are excavated by the bats (Kalko et al. 2006). The resulting cavities are inhabited by small groups of an average of 4–8 bats (maximum 19—Dechmann et al. 2005; Ueberschaer 1999). In spite of their roosting in termite nests, DKND found no evidence in the feces of *L. silvicolium* that termites are part of the bats' diet. In fact, the cavity inhabited by the bats is sealed off by the termites, who never enter it while the bats are present, as could be seen on video recordings. Instead, the termites close all tunnels damaged by the excavation of the nest, creating a surface similar to the outer skin of the nest.

All data that we review here were collected at 2 sites between 1998 and 2003. The 1st site was Barro Colorado Natural Monument, Panama. Most of the fieldwork there was done on Barro Colorado Island at the center of Barro Colorado Natural Monument. This 1,560-ha island is located in Gatun Lake (9°10'N, 79°150'W) and borders the Panama Canal in central Panama. Barro Colorado Natural Monument is covered with semideciduous tropical lowland rain forest (Foster and Brokaw 1982). Rainfall averages 2,600 mm per year, and about 90% of this falls during the rainy season from mid-April to December (Windsor 1990). The 2nd study site was located in the 22,000-ha Soberania National Park (9°07'N, 79°42'W) and was covered with similar vegetation as the Barro Colorado Natural Monument. Soberania National Park stretches along the mainland border of the Panama Canal, east of Barro Colorado Island.

TABLE 2.—Comparison of ectoparasites on *Lophostoma silvicolum* and a closely related and morphologically as well as ecologically similar species living in tree cavities (*Tonatia saurophila*).

	<i>Lophostoma silvicolum</i> ($\bar{X} \pm \text{SD}$)	<i>n</i>	<i>Tonatia saurophila</i> ($\bar{X} \pm \text{SD}$)	<i>n</i>	Mann–Whitney <i>U</i> -test		
					<i>U</i>	<i>U'</i>	<i>P</i>
Wing mites	3.62 \pm 5.84	210	9.93 \pm 13.4	91	6,497.0	6,497.0	<0.0001
Streblid flies	0.79 \pm 1.67	244	1.92 \pm 2.99	60	5,531.5	9,108.5	0.0029

BENEFITS OF ROOSTING IN TERMITE NESTS

For our study, regardless whether males or females make roosts, it was important to determine 1st whether termite nests are advantageous in comparison to roost types more commonly used by other bat species, such as tree holes, to justify the time and energy investment required for the excavation. There are many potential advantages to roosting in termite nests, including protection from predators, proximity to foraging areas, reduced parasite loads, reduction of intra- and interspecific competition, and, most of all, a beneficial microclimate, which is particularly important for reproductive female bats (Kunz 1982; Kunz and Lumsden 2003; Lewis 1995). In *L. silvicolum*, the 3 parameters that we investigated—availability of suitable termite nests (Kalko et al. 2006), ectoparasite load (data included below), and roost microclimate (Dechmann et al. 2004)—suggest that excavated termite nests are highly desirable shelters.

Nest availability.—The obligate tie of *L. silvicolum* to its host may limit the bats' geographical distribution to that of the termites. However, the criteria bats use to determine nest suitability and whether availability of such nests was limited remained unclear. In a census of termite nests on 2 plots on Barro Colorado Island, Kalko et al. (2006) recorded a set of 15 descriptive nest parameters. They then compared nests from the census with 44 excavated nests according to these parameters and found that suitable nests were active, medium sized ($>30 \times 30$ cm), shaded, have few or no branches leading through them, and are free of vegetation immediately below the opening of the cavity at the bottom of the nest. Thirty-nine nests in the census met all criteria, but only 5 of them had a bat-made cavity. Thus, availability was much greater than use by the bats and density of *L. silvicolum* on Barro Colorado Island is probably limited by other factors.

Ectoparasite load.—There are 2 major groups of bat ectoparasites at our study site: streblid flies (Streblidae) and wing mites (Acarina). Streblids are transmitted via pupae on the roost wall and may be the reason that some bat species frequently switch roosts (Reckardt and Kerth 2007; ter Hofstede and Fenton 2005). Wing mites are transmitted through direct physical contact between bats. Generally, loads of contact-transmitted ectoparasites increase with group size (Coté and Poulin 1995). This may be particularly true for reproductive female bats, which have depressed immune systems, often accompanied by an increase of ectoparasites (Christe et al. 2000; Lourenço and Palmeirim 2007). The energetic or reproductive costs of higher ectoparasite loads in bats have rarely been quantified but they can result in higher grooming costs in nonreproductive bats (Giorgi et al. 2001). Examination of previously unpublished data presented here shows that *L.*

silvicolum has significantly lower ectoparasite loads of both types of parasites than a similarly sized, closely related, and ecologically similar species, *T. saurophila*, roosting in tree cavities (Table 2). The lower ectoparasite loads may be an indirect benefit of the chemical defenses against parasites for which termites are known (Prestwich 1988).

Microclimate.—It can be crucial for reproductive female bats to minimize daily energy expenditure through the selection of warm roosts (Racey and Speakman 1987; Tuttle 1975; Wilde et al. 1999). Despite this important role of roost microclimate for bats, little is known about the thermoregulatory advantages that may be gained by roost making. Old World termites are well known for intricate manipulation of mound microclimate through both their nest architecture and metabolism within mounds (Korb and Linsenmair 2000). If the same were true for nests of the neotropical *N. corniger*, Dechmann et al. (2004) predicted that temperature in the cavities made by *L. silvicolum* would be higher and more stable than in tree cavities used by other bats. Energy saved through this roost choice might play a critical role in the evolution of roost making by *L. silvicolum* and other animals living in termite nests. In addition, we hoped that the temperature regime would offer an explanation for the observation that the bats leave their excavated termite nests whenever the insect colony dies. Although temperatures were very stable in both tree cavities and termite nests, temperatures inside active termite nests were 2.1–2.8°C warmer than in tree cavities (Fig. 1). In addition, temperatures were both more stable and higher in active than in inactive termite nests (Dechmann et al. 2004). This significant difference was independent of location of the roost in the study area or season. After we established that microclimates of roosts in termite nests are indeed beneficial and superior to those of tree cavities, but only while the termite colony was alive, it became necessary that we assess who was actually excavating the roosts—males, females, or both—in order for us to understand the link between this roost choice and the social system, and perhaps also to understand the mating strategy of these bats. In Table 1 we have summarized and outlined predictions concerning behavior of both sexes, behavior of males, morphology, and physical condition, as well as female group composition, genetic structure, and dispersal of offspring, depending on the main selective pressure promoting roost making: sexual selection or natural selection.

WHO ARE THE ROOST MAKERS AND WHAT IS THEIR FITNESS BENEFIT?

Behavior of both sexes.—Group composition reflects the social organization and often mating system of a species. In

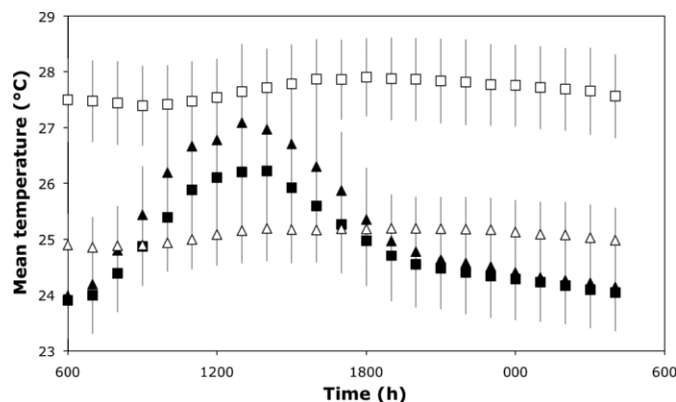


FIG. 1.—Temperatures inside (open symbols) and outside (filled symbols) active termite nests (squares, $27.9^{\circ}\text{C} \pm 1.0^{\circ}\text{C}$, mean \pm SD, $n = 10$) and tree holes (triangles, $25.1^{\circ}\text{C} \pm 0.5^{\circ}\text{C}$, $n = 5$) measured over 1 week. Temperatures in termite nests are significantly higher than in tree cavities inhabited by species closely related to *Lophostoma silvicolum*. Mean inside temperatures of both roost types are more stable than ambient temperatures. Figure adapted from Dechmann et al. (2004).

a polygynous mating system typically only 1 reproductively active male would be present in a social group during the mating season, although subordinate or satellite males also can be present (Ortega and Arita 2002; Voigt and Streich 2003). In a social system more reminiscent of maternity colonies of temperate bat species and with roost making by females, one would expect any reproductively active males to be absent in the roost or to be present only during the mating season. Dechmann et al. (2005) captured groups of *L. silvicolum* 61 times from 34 excavated nests during all seasons. Capture data were always consistent with a single-male-multifemale social system. It was not always possible to catch all bats present in the roosts, but there was never more than 1 adult male (except in bachelor groups), and in all cases where there was no male, at least 1 individual had escaped.

Dechmann et al. (2005) also recorded nocturnal behavior in 2 bat-made cavities in termite nests with infrared video to determine sex and identity of nest excavators. All bats in the study were marked using passive integrated transponders (PIT tags; Euro ID, Weilerswist, Germany) implanted subcutaneously. Automatic antennae (handmade by DKND) placed around the roost entrance, and attached to a logger (Euro ID) recorded the identity of each bat entering and exiting. In a total of 19 nights, nest excavation was recorded on 5 nights (2–35 min each). In addition, an unmarked male was filmed working on the termite nest and on the stump of a branch that had led through it for >2.5 h. In all nest excavation events, the male excavated only when females and juveniles were not present in the roost (Dechmann et al. 2005). On each of those occasions the single adult male in the nest repeatedly bit into the cavity wall with his canines and then pushed himself off with his wrists, breaking off small pieces of nest material in the process. Many bat species remain in their foraging areas throughout the night. However, both male and female *L. silvicolum* always

return to the roost for nocturnal breaks from foraging (Lang et al. 2006). Thus, the male not only invests physical energy in roost making, but he also spends less time foraging than the females. This is an additional indicator of a high male investment, which is typical for a resource-defense polygynous mating system.

Morphology, behavior, and reproductive success of males.—In most bat species investigated to date, there is no sexual dimorphism or, if there is sexual dimorphism, females are slightly larger than males. This is probably due to the fact that most studies were conducted in the temperate zone, where many species mate more or less promiscuously and females give birth to very large young that must reach adulthood before the next hibernation period (Myers 1978; Ralls 1977; Rossiter et al. 2006; Williams and Findley 1979). A very interesting tropical example is the flying fox *Cynopterus sphinx*, where sexual dimorphism switches from larger females to larger males along a latitudinal gradient. This reversal is inversely correlated with the distribution of polygyny in this species (Storz et al. 2001). In polygynous mammals with a strong reproductive skew among males, females are usually the smaller sex (Ralls 1977). This is especially the case when the males have to invest a large effort into courtship or into the creation and defense of a resource or a harem or both (Lindfors et al. 2002; Weckerly 1998). In *L. silvicolum*, males were significantly larger than the females in 3 standard size parameters (length of forearm, length of tibia, and body mass—Dechmann et al. 2005). Consistent with this result was the finding that 21 males who successfully excavated a termite nest were in significantly better body condition (relative body mass corrected for size measured by forearm length) than 33 bachelor males, the former being >2 g heavier on average (6–7%—Dechmann et al. 2005). This may have several non-exclusive reasons. Only males in good physical condition may be able to spare the energy required to excavate, maintain, and defend a cavity (e.g., in fallow bucks [*Dama dama*] only strong males can defend a harem—McElligott et al. 2003). Females also may choose a mate according to his physical condition. Finally, there could be an additional age effect, with older males being heavier and thus better able to excavate and defend a roost.

The data presented above support the hypothesis of the evolution of roost making in *L. silvicolum* under sexual selection for at least 2 reasons. First, single males excavate the termite nests, investing time and effort to provide a beneficial resource for females. Second, females seem to choose a male according to his physical condition as well as his possession of a roost. The roosts appear to act as an extended male phenotype, making it easier for the females to judge male quality, but also to locate a high-quality male via his nest. This scenario only makes sense if the females then also mate with the male owning a roost. If roost making improves the mating success of males, the evolution of such a trait would be enhanced (Andersson 1994). Even though sexual selection seems to be the dominant driving force for the evolution of this behavior, natural selection cannot be completely excluded. Females and young, and also the males, probably profit from

the warm and stable microclimate and reduced ectoparasite loads, which may directly improve fitness of both sexes.

Female *L. silvicolium* exhibit postpartum estrus (i.e., they become fertile shortly after they give birth to a young). If the females are very mobile and exhibit low or no group stability, an unlucky male might be joined only by pregnant females, which then give birth to another male's young in the roost he so elaborately provided (Fig. 2). Termite nests, in spite of all their advantages, can be destroyed by anteaters (*Tamandua mexicana*), tree falls, decay as a consequence of death of the termite colony, or other natural causes, and nest longevity can vary from a few months to several years (Dechmann et al. 2007). Females are thus fairly often forced to switch roosts and males must excavate new ones. Reproduction by females is highly synchronized and seasonal (Dechmann et al. 2005); thus infanticide by males would not speed up the female's reproductive cycle and the male's access to mating. Consequently, even though sheltering another male's offspring in the roost does not incur additional cost, only a relatively high reproductive success at the next postpartum estrus can explain the evolution of roost making by the males.

Dechmann et al. (2005) determined reproductive success of males with 2 measures: number of young they sired and average relatedness of each male to young in his own nest compared to the same male's relatedness to young in other nests. They were able to assign 21 of 46 young to the predicted father, corresponding to a reproductive success of 46%. Males sired 0–4 of 5 young in their own roost per reproductive season. This is probably a low estimate, as for paternity assignments it is necessary to predict putative fathers. Most mothers were captured only once and thus it was impossible to determine whether they had switched roosts since the last reproductive season. However, 17 of the 21 mothers were still roosting with the father of their young. This shows that, although females switch roosts quite easily, they commonly stay with the same male for several reproductive seasons if undisturbed, thus providing a stronger motivation for the male to invest in roost making. According to anecdotal evidence, females may also move to a new roost together with a male when the old roost is destroyed (Dechmann et al. 2007).

In the 2nd analysis, Dechmann et al. (2005) compared average relatedness of males ($n = 12$) with all young born in their roost with all young born in other males' roosts, thus testing for scenarios such as roosts 2 and 3 in Fig. 2. Males were significantly more closely related to young caught in the same roost than to young from other roosts.

A consequence of polygyny is that a few males monopolize the majority of matings, whereas most males gain little or no access to females. A reproductive success of 46% and a 25% average relatedness to young in their roost thus seems to justify a high investment of time and energy by the males. These values also fall well into the range of relatedness found in other polygynous bat species (e.g., 29% in *S. bilineata* [Heckel et al. 1999] and 69% in *A. jamaicensis* [Ortega et al. 2003]). Extraharem reproductive success, which plays an important role in the bat species mentioned above and which may further

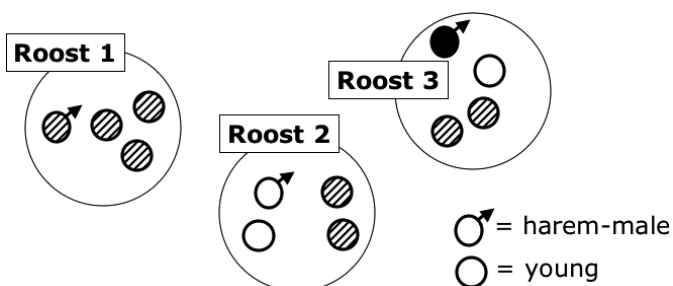


FIG. 2.—Three potential outcomes regarding reproductive success of a nest-making male *Lophostoma silvicolium*. Same shading indicates genetic relatedness. In roost 1, all young born in his roost are sired by the nest male (mothers did not leave since the last reproductive season); in roost 2, 1 young was sired by the nest male, and 2 by other males (their mothers mated outside the roost or recently joined the group already pregnant); and in roost 3, all young were sired by other males.

increase the reproductive success of harem males, was not assessed for *L. silvicolium* and cannot be distinguished from matings with previous, uncaptured harem males.

There was always only 1 adult male in each of the groups caught from termite nests, implying that male offspring of *L. silvicolium* invariably disperse. In some species of polygynous bats subordinate or satellite males, or both, can be found, especially in larger harems (Ortega and Arita 2002; Voigt and Streich 2003). They are usually related to the dominant harem male and take over the group of females when he is removed (Voigt and Streich 2003). It could have been possible that young males of *L. silvicolium* disperse but then establish a roost and territory near those of their father to indirectly profit from his defense of the territory. However, Dechmann et al. (2007) conducted a Mantel test that investigated the relationship between distance between roosts and pairwise relatedness of males. The results showed that there is no correlation between the 2 factors. This is in spite of the fact that roosts of (nonrelated) males can be as close as 25 m to each other. Males probably randomly settle wherever they find a suitable nest for excavation. The male's resource ensuring his reproductive success is the cavity he makes and not a territory (forest patch). In fact, foraging areas of males from neighboring roosts have been found to overlap in a telemetry study (Bockholdt 1998).

Another parameter typical for polygyny is strong reproductive skew among males. This was not assessed directly for *L. silvicolium*. However, roost captures revealed significantly higher numbers of females. In contrast, numbers of males and females caught in mist nets at random sites in the forest did not differ (Dechmann et al. 2007). Consequently, the female-biased sex ratio in the roosts is not due to different survival rates of the sexes. No young were assigned to males from bachelor roosts and roost males accounted for almost 50% of the young. All of the above are consistent with a strong reproductive skew, further supporting the hypothesis of roost making evolving under sexual selection, resulting in a unique form of resource-defense polygyny.

Behavior and genetic structure of female groups, and dispersal of offspring.—The evidence outlined above is consistent with the hypothesis that males excavate roosts in termite nests to improve reproductive success, as expected in resource-defense polygyny. This in turn may have implications for the social organization of the females (Table 1). There may or may not be philopatry of female offspring, depending on the degree of cooperation between female group members or other benefits of natal philopatry such as familiarity with the habitat. In fact, many associations of bats are characterized by philopatry of female offspring or both male and female offspring, although 1 case where only male offspring are philopatric also is known (male and female philopatry in *Plecotus auritus* [Burland et al. 2001], female philopatry in *Myotis myotis* [Castella et al. 2001], *Myotis bechsteinii* [Kerth et al. 2000], *Desmodus rotundus* [Wilkinson 1985b], and male philopatry in *S. bilineata* [Nagy et al. 2007]). However, matings take place outside the roost in most of those species. Philopatry of female offspring in outbreeding bats should be reflected by a high diversity in nuclear DNA but a very low diversity in mitochondrial DNA (Kerth et al. 2000, 2002).

Genetic diversity in *L. silvicolus* does not follow this pattern. Instead, both nuclear and mitochondrial DNA diversity was close to 1 and thus very high ($n = 75$ adult females from 14 groups; tested with 10 polymorphic microsatellite [= nuclear] loci and the mitochondrial D-loop—Dechmann et al. 2007). In addition, a genetic assignment of all adult *L. silvicolus* caught in roosts ($n = 159$) to each other revealed only 8 possible parent–offspring pairs that had been caught in the same roost, only 5 of which were caught from the same roost simultaneously. Examination of these data indicates that both sexes of offspring disperse from the natal roost before they reach adulthood. This is in accordance with the resource-defense mating system in conjunction with relatively long male tenure (up to 36 months) compared to the time it takes females to become sexually mature (at an age of 6 months or more—Dechmann et al. 2007). Young females may have to disperse to avoid inbreeding with their own father (Clutton-Brock 1989a), whereas young males may disperse to gain access to breeding partners and possibly also because they are expelled by the resident male (Dobson 1982; Greenwood 1980).

In addition, Dechmann et al. (2007) tested genetic structure between the same social groups. Here the prediction would have been the opposite from within-group diversity: if there was female philopatry, female groups should be strongly differentiated genetically. Pairwise differentiation between the F_{ST} -values of mitochondrial haplotypes of groups of females always was nonsignificant. Similarly, 98 of 105 pairs in a comparison of microsatellite genotypes showed no significant difference before Bonferroni correction, indicating high levels of gene flow between groups. However, there was a negative influence of distance between roosts on the average F_{ST} -values for nuclear DNA of female groups (Dechmann et al. 2007). Female offspring left the parental roost but settled nearby, because the danger of accidentally choosing a roost occupied by a related male was independent of distance (see above).

Thus, females may profit from familiarity with their natal area when dispersing.

Both sexes of offspring disperse in *L. silvicolus*, probably as a consequence of the species' mating system. This dispersal pattern results in high genetic diversity within social groups, which should be reflected by the behavior among group members (Kerth 2008). In groups of flexible composition few or no social interactions among group members are expected (e.g., Fleming et al. 1998). In contrast, cooperation is expected in stable female groups (e.g., Kerth et al. 2003; Ortega and Maldonado 2006). In the latter species, females engage in allogrooming.

We also made video recordings from the same roosts of *L. silvicolus* as were observed for nest excavation. These recordings were made during all seasons of the year to exclude potential seasonal effects, and they were analyzed ($n = 12$ full nights from 1st emergence to sunrise) to determine social interactions between females in the roosts. The 1st roost contained 1 adult male, 3 adult females, and 2 juveniles. The 2nd roost consisted of 1 adult male and 3–5 females. Both groups were thus typical harems. The only social interaction between group members occurred when individuals returned to the roost, especially during the first 60 s, and consisted of the returning bat presenting its belly to be sniffed by bats already present in the nest. This interaction was particularly intensive between the male and each female. The resident male once expelled a strange male from the roost, although a female was allowed to join the group after having been sniffed particularly intensively by the resident bats in the roost. Social interactions indicating cooperation or any kind of close bond such as allogrooming between females were never observed.

GENERAL DISCUSSION

This review provides evidence that roost making in *L. silvicolus* is strongly influenced by sexual selection by females for male-excavated roost cavities in termite mounds. In addition, natural selection acting on males may have further enhanced the evolution of the use of this roost type through a beneficial microclimate and reduced parasite loads. Males excavate the termite nests and thus pay the entire costs of this behavior. Harems are composed of females, with each harem aggregating in the roost of 1 male. Indeed, one of us (DKND) observed that almost all females usually leave a roost after a capture attempt, probably a similar experience to an attack on the nest by a predator, whereas the male usually returns. Thus, female roost fidelity is lower than that of males, showing that roost availability through male excavating behavior is very important for the social system of this species.

Many tropical bats, including all known roost-making species, live in single-male–multifemale associations (Kunz et al. 1994; McCracken and Wilkinson 2000) and probably have polygynous mating systems. Is roost-making behavior a sexually selected male trait in all of these species? Tent making is the most common form of roost making in this order, but the process of the actual making of a tent has very rarely been observed in the field (Kunz et al. 1994). However, the few

available studies indicate that male roost making is usually, but not always, the case (Balasingh et al. 1995; Rodríguez-Herrera et al. 2006). For example, in *Ectophylla alba* from the same family as *L. silvicolium* (Phyllostomidae), which also lives in single-male-multifemale societies, females have been recorded manipulating the roost leaf to construct a tent with no observed contribution of males. This indicates that at least in this species roost making might be a cooperative behavior of females and thus naturally selected (Rodríguez-Herrera et al. 2006). Knowledge about the advantages of roosting in leaf tents, as well as the mating system and genetic group composition of such species, will help us to better understand roost making in general.

Lophostoma silvicolium exclusively roosts in excavated active termite nests and thus is an example of a species with a single social system associated with the roost choice. However, this is not true for all roost-making bats. For example, *A. jamaicensis* regionally switches between the use of leaf tents, probably made by the bats (Kunz and McCracken 1996), to naturally occurring tree cavities or solution cavities in caves (Ortega and Arita 1999, 2000). *A. jamaicensis* always lives in harems, but the stability and composition of female groups is known only from cave-dwelling populations. However, in all roost types, defense of roosts has been observed and it will be interesting to see if the mating system of *A. jamaicensis* is always a female-defense polygyny. This in turn depends on high stability of female groups, which may be decreased in more temporary roosts such as tents (Lewis 1995). Another group of bats with facultative tent making are the Old World flying foxes of the genus *Cynopterus*. In *Cynopterus* the use of naturally occurring or bat-made tents depends on local availability of resources. When resources are clumped and spaced, tent making is more common and female groups are more stable, but wherever resources allow, naturally occurring, unmodified roosts are used (Campbell et al. 2006a, 2006b). In *C. sphinx* there is additional variation in the mating system, and the direction of sexual dimorphism depends on latitude (Storz et al. 2001). Nonetheless, when tent making occurs in *C. sphinx* and *C. brachyotis* it is done by single males and the process can be very elaborate and time consuming. Thus, roost making does seem to be a sexually selected trait in this genus (Balasingh et al. 1995; Bhat and Kunz 1995; Tan et al. 1997). Perhaps roost making evolved several times in polygynous systems and due to different reasons in each species of roost-making bat.

In addition, a number of non-roost-making phyllostomids seem to live in resource- or female-defense polygynous systems (Heckel and von Helversen 2003; McCracken and Bradbury 1977, 1981; Ortega and Arita 2000; Ortega et al. 2003). But even here the degree of stability of female groups varies and the females of some of these species use long-lasting roosts, where they form long-term stable associations (see also above), which can be combined with cooperation among group members (Ortega and Maldonado 2006; Wilkinson and Boughman 1998). The most extreme case is the common vampire bat, *D. rotundus*, where females have been observed regurgitating blood and otherwise cooperating with nonrelated group members (Wilkinson 1984, 1986, 1990). Female

cooperation seems to be so important in this species that females have found alternative, yet unexplained, ways to avoid inbreeding. Female offspring are philopatric even though male tenure is longer than it takes them to reach sexual maturity. In contrast, male offspring are forced by the dominant male to leave the roost (Wilkinson 1985a, 1985b). The opposite is the case in *S. bilineata*, a well-studied species with resource-defense polygyny (see also Voigt et al. 2008). Here, females also form long-term stable groups, but no cooperative behavior is known (Heckel and von Helversen 2003). However, female offspring disperse, whereas males can be philopatric and queue for harem access (Nagy et al. 2007; Voigt and Streich 2003). Males of this species do not provide roosts, but exhibit very elaborate courtship behavior. Nonetheless, extraharem paternity is high. Extraharem mating may be a strategy of the females, which have been in the harem for several years, to avoid mating with their sons.

The more we learn about roost-making behavior and the social systems of bats, the more it becomes clear that an enormous amount of work remains to be done. Roost making can be a sexually selected male trait as in *L. silvicolium*, or, it appears, a naturally selected female behavior as in *E. alba*. It will be intriguing to test other species according to the characteristics listed in Table 1 to determine their social systems and mating strategies. Detailed studies on additional species and variation within species will teach us more about the evolution of the making of shelters and contribute to our general understanding of the evolution of sociality in mammals.

CONCLUSIONS

Here, we review the literature on the social and mating system of *L. silvicolium*, a roost-making bat, which modifies an unusual type of structure, active termite nests. We try to determine, in particular, whether natural or sexual selection was the main driving force during the evolution of roost-excavating behavior. We show that this roost choice is closely linked to the bats' social organization, single-male-multifemale associations, and to their mating system, resource-defense polygyny. Single males invest large amounts of time and energy to provide a roost, gaining access to matings with the females who join them. Females in turn choose the male according to his physical condition among roost-owning males, but do not form closed groups or show any kind of cooperative behavior. Both sexes of offspring disperse, resulting in a genetically homogenous population, where the choice about where to settle for both males and females depends on suitable termite nests (and possibly other ecological factors such as foraging areas), but not on social context. Roost making in *L. silvicolium* is clearly under sexual selection and the roosts can be regarded as an extended male phenotype. Our comparison with other roost-making species shows variation in social systems and dispersal behavior from species to species. This indicates multiple potential origins and courses of evolution of roost-making bats. Future studies on bats and other mammals will help us to better understand the implications and thus the evolution of making of shelters for social and mating systems.

RESUMEN

Los refugios son importantes para la sobrevivencia y reproducción de muchos animales, y esto es particularmente cierto para los murciélagos. Dependiendo del uso futuro y el efecto de los refugios en la adecuación de los individuos, no todos los miembros de los animales podrían contribuir equitativamente a hacer el refugio. Por lo tanto, el conocimiento de la identidad de los individuos que hacen el refugio podría enseñar mucho sobre del sistema social y del sistema de apareamiento. Para evaluar esto, se hizo una revisión de lo que se conoce acerca la conducta para hacer refugios y el sistema social de *Lophostoma silvicolum*, un murciélago neotropical que excava sus refugios en nidos de termitas activos. Los refugios en nidos de termitas son de gran beneficio para los murciélagos porque ofrecen un mejor microclima y están probablemente relacionados con una carga de parásitos más baja que en especies que usan otros tipos de refugios mas comunes. Observaciones de campo y análisis genéticos mostraron que los refugios, que subsecuentemente sirven de refugios de maternidad, son excavados por un sólo macho y que esto aumenta el éxito reproductivo del macho que hizo el refugio. Esto sugiere que los refugios en nidos de termitas sirven como una extensión del fenotipo del macho y que la construcción de refugios es una conducta seleccionada sexualmente. La conducta de construcción del refugio esta fuertemente ligada a la organización social de la especie (asociaciones de un macho con varias hembras que se mantienen juntos todo el año) y el sistema de apareamiento (poliginia por defensa del recurso). El caso de *L. silvicolum* muestra que es importante entender mejor las implicaciones de la construcción de refugios en murciélagos y otros animales en estudios futuros. Sin embargo, diferencias en costos-beneficios para cada miembro del grupo debe ser evaluadas cuidadosamente antes de inferir conclusiones acerca del sistema social y las estrategias de apareamiento, para contribuir al conocimiento de la evolución de la sociabilidad en mamíferos.

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